Morphology of trophic eggs and ovarian dynamics in the subsocial bug *Adomerus triguttulus* (Heteroptera: Cydnidae)

Shin-ichi Kudo, Taichi Nakahira, and Yutaka Saito

Abstract: In the subsocial burrower bug, *Adomerus triguttulus* (Motschulsky, 1886), females produce trophic eggs, which are inviable and serve as a food supply for hatched nymphs, and add them onto egg masses during maternal care. Trophic eggs are expected to be less costly for females to produce and for offspring to consume than viable eggs. Such specialization may be reflected in the size, structure, and developmental process of the eggs. Inviable trophic eggs were smaller than viable eggs, and the intraclutch size variation of the former was larger than that of the latter. The viable eggs always had approximately five micropylar processes at a pole, whereas the trophic eggs mostly lacked them. Active oogenesis was maintained during the maternal egg care period; oocyte development continued after the deposition of viable eggs and declined close to the hatching time of the clutches. Mature chorionated eggs were consistently observed in ovaries. It is strongly suggested that at least some trophic eggs contained in clutches at hatching are those that have matured and been deposited during the maternal care of eggs. We discuss possible selective factors leading to the specialization of these unusual heteropteran trophic eggs and the ecological significance of their ovarian dynamics.

Résumé : Chez la punaise mineuse subsociale *Adomerus triguttulus* (Motschulsky, 1886) (Heteroptera : Cydnidae), les femelles produisent des oeufs trophiques non viables qui servent de ressource alimentaire aux larves nouvellement écloses; les femelles les ajoutent aux masses d'œufs lors des soins maternels. Les oeufs trophiques sont reconnus comme moins coûteux à produire par les femelles et à consommer par les rejetons que des oeufs viables. Cette spécialisation peut se refléter dans la taille, la structure et le processus de développement des oeufs. La taille des oeufs trophiques non viables est plus petite et leur variation de taille dans une même masse d'oeufs plus grande que celle des oeufs viables. Les oeufs viables possèdent toujours à l'un des pôles environ cinq structures en micropyle, alors que la plupart des oeufs trophiques n'en ont pas. L'ovogenèse active se continue durant la période de soins maternels des oeufs; le développement des oocytes se poursuit après la ponte des oeufs viables et diminue près de la période de l'éclosion des oeufs. Il y a constamment des oeufs chorionés matures dans les ovaires. Nous sommes fermement convaincus qu'au moins certains des oeufs trophiques présents dans les masses d'œufs au moment de l'éclosion sont ceux qui se sont développés et qui ont été pondus durant la période de soins maternels des oeufs. Nous discutons des facteurs possibles de sélection qui mènent à la spécialisation de ces oeufs trophiques inhabituels chez les hétéroptères et de la signification écologique d'une telle dynamique ovarienne.

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Introduction

In a variety of arthropods, siblings often eat eggs within clutches (Polis 1981). Sibling oophagy such as this is usually associated with hatching asynchrony and unsuccessful hatching, including infertile eggs (e.g., Kawai 1978). However, functional differentiation of victim eggs has also been reported; they are inviable and are usually supplied as food. Such inviable eggs are referred to as trophic eggs (Crespi 1992).

S. Kudo.[1] Department of Biology, Naruto University of Education, Naruto, Tokushima, 772-8502 Japan.
T. Nakahira. Systematic Entomology, Faculty of Agriculture, Hokkaido University, Sapporo, 060-8589 Japan.
Y. Saito. Laboratory of Animal Ecology, Department of Ecology and Systematics, Hokkaido University, Sapporo, 060-8589 Japan.

[1]Corresponding author (e-mail: skudo@naruto-u.ac.jp).

Trophic eggs are well known in several groups of eusocial insects, the order Hymenoptera (Sakagami 1982; Hölldobler and Wilson 1990; Crespi 1992; Wheeler 1994). Often they have not only a different function but also a distinctive morphology from viable eggs (e.g., Koedam et al. 1996; Gobin et al. 1998). There are also a few non-eusocial insect orders that include species that produce trophic eggs, i.e., Coleoptera (e.g., Perry and Roitberg 2005), Neuroptera (Henry 1972), Orthoptera (West and Alexander 1963), Heteroptera (Hironaka et al. 2005), and possibly Psocoptera (Mockford 1957; reviewed by Crespi 1992; Perry and Roitberg 2006). Trophic eggs can be differentiated as being less costly than viable eggs for females to produce (but sufficient in nutrition) and for offspring to consume (Crespi 1992). Such specialization may be reflected in the size, structure, and developmental process of the eggs. A comparative analysis of the specialization of trophic eggs among insect lineages with different reproductive histories should provide significant insight into the adaptation and evolution of trophic eggs.

Nakahira (1994) reported that females of the burrower bug, *Adomerus triguttulus* (Motschulsky, 1886) (Cydnidae),

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produce egg clutches containing inviable trophic eggs. This was the first discovery of trophic-egg production in the order Heteroptera, and another example has recently been added (Hironaka et al. 2005). Like other subsocial cydnid bugs (Filippi et al. 2001), *A. triguttulus* females show complex maternal care of eggs and nymphs (Nakahira 1992, 1994). The nymphs feed upon trophic eggs soon after hatching and gain nutritional benefits (Kudo and Nakahira 2004). Kudo and Nakahira (2005) have shown that females can adjust trophic-egg production in an adaptive manner: they increase relative trophic-egg investment under poor food-resource conditions. As well as the timing of nutrient intake, ovarian dynamics provide clues to proximate mechanisms concerning the plasticity of reproductive resource allocation (e.g., Boggs 2003; Jervis et al. 2005). In this paper, we describe the morphological differentiation of trophic eggs and ovarian development in this unusual heteropteran species.

Materials and methods

Reproductive history of *Adomerus triguttulus*

Post-hibernation *A. triguttulus* adults appear on host plants, mint (*Lamium*) spp., from May to June in Sapporo, in the northern part of Japan (Nakahira 1992). Breeding is synchronized with the flowering phenology of each *Lamium* species. Females feed upon developing seeds on the plant to develop their ovaries and then move to the ground for oviposition. Under the leaf litter, the females deposit viable eggs and form their spherical egg masses almost within a day (Nakahira 1992, 1994). They attend to their egg masses and guard them against arthropod predators (Nakahira 1992).

During egg care, the females temporarily leave their eggs to feed upon seeds. They produce inviable trophic eggs and add them to the viable egg masses (Nakahira 1994). Nymphs feed upon the trophic eggs within a day after hatching (Kudo and Nakahira 2004). The trophic-egg feeding by hatched nymphs enhances their growth and survival (Kudo and Nakahira 2004). After hatching occurs, the females show progressive provisioning: they temporarily leave their broods and transport seeds to feed them. Maternal care usually ends within the second instar (Nakahira 1992).

Adomerus triguttulus is not an obligatory semelparous species: under laboratory rearing conditions, females raise more than one brood at approximately 30-day intervals (S. Kudo and T. Nakahira, unpublished data). However, it remains unknown whether or not such iteroparity is accomplished under field conditions.

Rearing

Gravid females were collected on *Lamium purpureum* L. and *Lamium album* L. on the Hokkaido University campus from May to June 1993. When the females were collected, no clutches were found in the field. Females were confined in plastic petri dishes (9 cm diameter, 1 cm height) containing filter paper and 10–20 host seeds and kept under 16 h light : 8 h dark, 20 °C conditions. Paper shelters were placed in each petri dish for oviposition sites. Under these conditions, viable eggs usually hatch on the 11th day after the start of oviposition (Nakahira 1994).

Measurement of eggs

The first clutches were used for the following analyses. On the 10th day after the start of oviposition, just before hatching occurred, we carefully separated eggs using a fine brush and forceps. Viable eggs were easily distinguished from inviable trophic eggs by possessing developed embryos with pigmented eyespots at the time close to hatching. Eggs that possessed no visible structure at that time were kept on the filter paper in the petri dish for at least 10 days and were then judged as to whether they were viable or not. Viable eggs do not show any remarkable changes in mass during development (Nakahira 1994). We measured the length and the width of viable and inviable eggs from each clutch under a dissecting microscope using an ocular micrometer at 25× magnification. The egg volume was estimated, as eggs are prolate ellipsoids. A few eggs that had been damaged during separation were excluded from the measurements. The numbers of viable and inviable eggs measured in each clutch were, on average, 71.60 ± 25.21 (SD) and 29.19 ± 8.44, respectively. Moreover, we randomly selected five viable and five inviable eggs from each clutch and carefully examined the number of micropylar processes (micropyles) on the egg surface. The mean values and standard deviations of measurements of eggs from each clutch were used in the statistical comparison of morphology between viable and inviable trophic eggs.

Viable and inviable eggs were also observed using a scanning electron microscope (SEM) (Hitachi S-2100A). The egg samples were prepared as non-coated specimens (namely "wet" SEM observation) to observe the precise nature of the chorion morphology.

Ovarian development during egg care

To monitor ovarian development during egg care, we dissected females just after (within 24 h) the start of oviposition ($N = 10$), 1 day after oviposition began ($N = 7$), at the 5th day of egg-clutch attendance ($N = 6$), and at the 10th day after the start of oviposition, just before hatching ($N = 6$). Developing oocytes that exceeded approximately 0.1 mm in length were clearly recognized in ovarioles under the microscope. We counted the numbers of developing oocytes and mature chorionated eggs for each female.
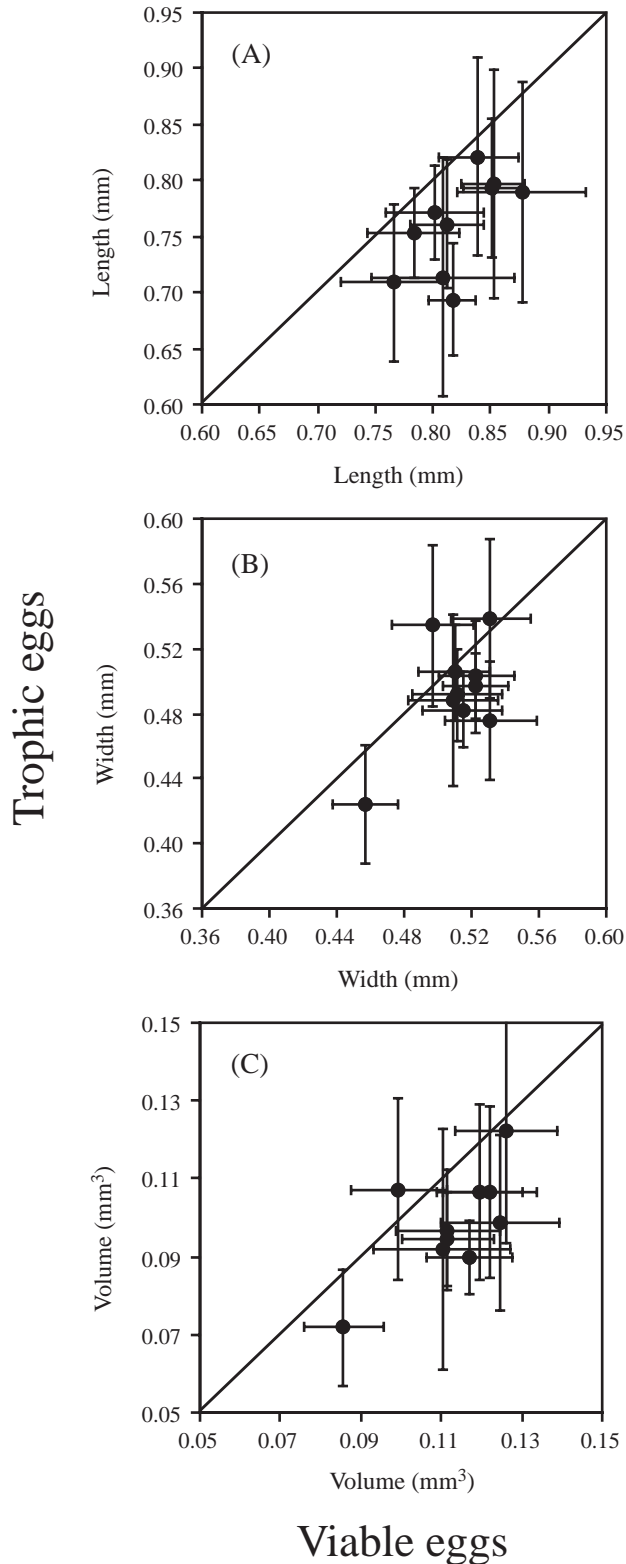
Results

Egg morphology

There were considerable variations in the size of viable and inviable eggs between clutches (Fig. 1). Viable eggs were significantly longer than inviable eggs (Wilcoxon's signed-ranks test, $N = 10$, $p = 0.005$), but there was no difference in width ($p = 0.09$) (Figs. 1A, 1B), suggesting that viable eggs were more oval and inviable eggs were more rounded. The volume of the former was 1.14 times greater than that of the latter ($p = 0.009$; Fig. 1C). There was a significant correlation between the volumes of viable and inviable eggs in a given egg mass ($r = 0.692$, $N = 10$, $p = 0.024$). No significant relationship was detected between clutch size and the volume (the cubic root) of viable eggs ($r = 0.521$, $p = 0.13$) or that of inviable eggs ($r = 0.297$, $p = 0.42$).

In addition, the size of both egg types varied considerably within as well as between clutches (Fig. 1). The coefficients of

Fig. 1. Comparison of length (A), width (B), and volume (C) between trophic and viable eggs of *Adomerus triguttulus*. Volume = $\pi/6 \times$ length $\times$ width^2. Each symbol on the graphs represents data (mean ± SD) for a clutch from a different female.

among viable eggs within clutches. When handled with forceps during measurement, neither viable nor inviable eggs collapsed, suggesting little difference in robustness between them.

Both viable and inviable eggs have thin chorions with smooth surfaces (Fig. 2). The viable eggs invariably had a ring of three to eight micropylar processes surrounding a pole (mean ± SD among 10 clutches = 5.36 ± 0.43; Fig. 2), whereas most of the inviable eggs lacked such structures (mean ± SD = 0.22 ± 0.37; Wilcoxon's signed-ranks test, $p = 0.005$). Only 4 of the 50 inviable eggs examined had micropylar processes; 2 had only one micropylar process and the other 2 had four and five, respectively, suggesting that the latter may be unfertilized rather than trophic eggs.

Ovarian development

Females' ovaries developed during the period of egg care (Figs. 3, 4). In some neuropterans, ovarioles are specialized to produce either viable or trophic eggs (Henry 1972), but such ovarian specialization does not occur in *A. triguttulus*.
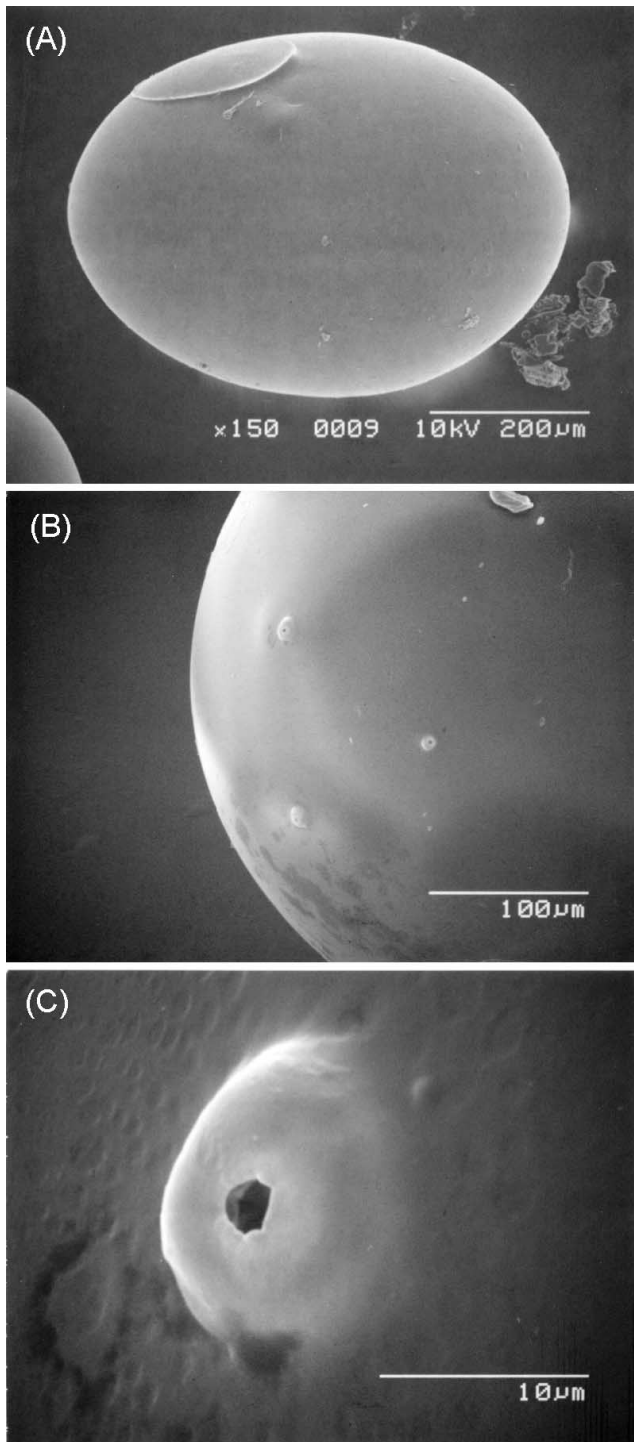
Mature chorionated eggs and a series of developing oocytes were always observed in the ovaries, which consist of 14 ovarioles (Fig. 3), and the number of the latter, but not the former, changed considerably with time after oviposition commenced (mature eggs, $F_{[3,25]} = 2.15$, $p = 0.12$; oocytes, $F_{[3,25]} = 33.61$, $p < 0.001$; Fig. 4). The number of developing oocytes in ovaries increased in the middle of the egg-care period, but by the 10th day, just prior to hatching, only a few developing oocytes were detected, indicating reduced oogenesis.

Discussion

Morphological differentiation

In *A. triguttulus*, inviable trophic eggs are morphologically different from viable eggs. A remarkable difference is that trophic eggs lack micropylar processes and micropyles. Follicle cells secrete chorion, and the chorionic apparatus is established at the end of oogenesis (Büning 1994). Considerable material and (or) energetic costs are expected in the formation of complicated chorionic apparatuses such as micropyles and micropylar processes. A lack of micropyles is also known in the trophic eggs of several other insect taxa (Henry 1972; Hölldobler and Wilson 1990; Koedam et al. 1996). The fact that trophic eggs were smaller than viable eggs in *A. triguttulus* also suggests that the former have a lower production cost. However, the relative size of trophic eggs is inconsistent among insect taxa. Trophic eggs are smaller than viable eggs in a related subsocial bug, *Parastrachia japonensis* Scott, 1880 (Hironaka et al. 2005). This is also the case for trophic eggs in a short-tailed cricket (West and Alexander 1963), owlflies (Henry 1972), and many ant species (e.g., Gobin et al. 1998). On the other hand, trophic eggs are larger in some species of stingless bees (Koedam et al. 1996) and ants (Hölldobler and Wilson 1990). Trophic eggs often have a thinner (or in some cases, no) chorion (Passera et al. 1968; Gobin et al. 1998) than viable eggs and are flaccid and easily ruptured (Brian and Rigby 1978; Koedam et al. 1996; Gobin et al. 1998; Gobin and Ito 2000). A thin and weak chorion would promote feeding efficiency in consumers and reduce production costs

variation (CV) for length (Wilcoxon's signed-ranks test, $N = 10$, $p = 0.005$), width ($p = 0.005$), and volume ($p = 0.005$) among inviable eggs were significantly larger than those

Fig. 2. Scanning electron micrographs of a trophic egg (A), micropylar processes on a pole of a viable egg (B), and a micropylar process, magnified (C).

Fig. 3. Ovaries of an *A. triguttulus* female. The female was dissected 48 h after the start of oviposition. Some mature chorionated eggs in the oviducts were removed.
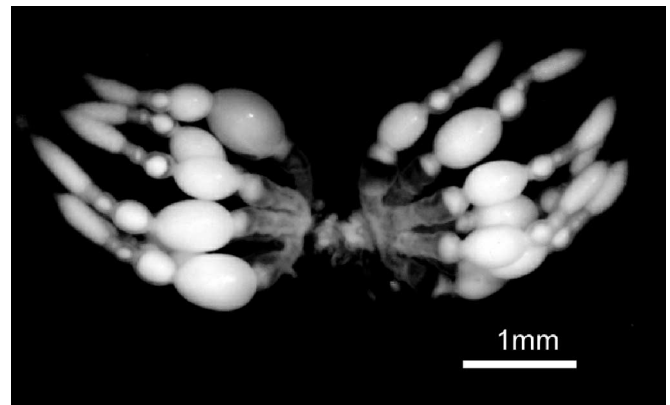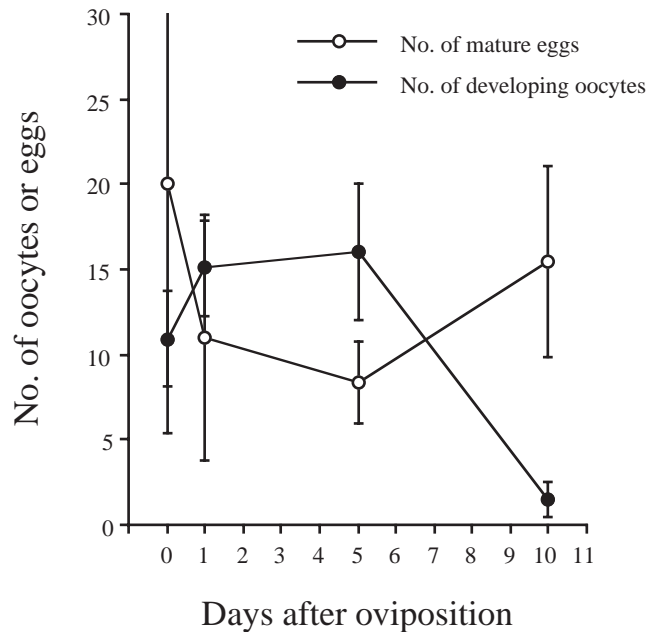

Fig. 4. Ovarian development during maternal care of eggs. Day 0 is the day when oviposition was confirmed. Hatching occurred on day 11. Means and standard deviations are shown.

for females. In *A. triguttulus*, however, trophic eggs did not greatly differ in robustness from viable eggs. Thus, there are differences in the morphological and structural specialization of trophic eggs among insect taxa, and these differences may be related to the functions of these eggs, which depend on different reproductive ecologies.

Hosts of *A. triguttulus*, *Lamium* spp., are myrmecophorous plants, the seeds of which are attached by elaiosomes (Beattie 1985), and there is high predation pressure by ants on and around these plants (Nakahira 1992). In addition to the lower cost of production, the smaller size of *A. triguttulus* trophic eggs may have resulted from unequal resource allocation among eggs within clutches in relation to such predation risks (Kudo and Nakahira 2004). Eggs on the peripheral surface of clutches are more vulnerable and thus females should invest less in such eggs than in those in the centre (Mappes et al. 1997; Kudo 2001). Trophic eggs of *A. triguttulus*, which are added to the surface of a viable egg cluster, may have originated from such "low-investment" viable eggs. The trophic eggs surrounding viable eggs could also have another function, i.e., as barriers against arthropod predators attacking viable eggs (Kudo and Nakahira 2004). In *P. japonensis*, trophic eggs located on the

periphery of egg masses would have a similar protective function (Hironaka et al. 2005).

If trophic eggs have such a protective function, in addition to providing nutrients for hatched nymphs, then their physical robustness should be more or less maintained. This may also be the case for *P. japonensis* and owlflies: their inviable eggs, "repagula", are hypothesized to protect viable eggs against ant predators (Henry 1972). On the other hand, the often flaccid trophic eggs of eusocial hymenopterans do not have any such protective function. The balance between different selection pressures decreasing the costs of production and consumption of trophic eggs as a food resource and increasing the benefits from other function(s), such as protective barriers for viable eggs, may affect the degree to which trophic eggs are specialized.

In *A. triguttulus*, trophic eggs were more variable in size than viable eggs, as suggested in some ant species (e.g., Brian and Rigby 1978; Gobin and Ito 2000). Although an optimal egg size could be selected for each population (Smith and Fretwell 1974), egg size often varies among females, among clutches produced by a single female, and even among individual eggs within clutches; the adaptive nature of such egg size variation is a controversial issue (Fox and Czesak 2000). The functions of *A. triguttulus* trophic eggs (i.e., nutrients for hatched nymphs and possible protective barriers for viable eggs) do not appear to be strongly affected by size per se, but rather by the total volume. Thus it is likely that the strength of the selection acting on the size of trophic eggs is lower than that acting on the size of viable eggs. This may explain the difference in the magnitude of size variation between trophic and viable eggs.

In some ant species, there are chemical differences between the contents of trophic and viable eggs (Wheeler 1994). Such chemical properties, in combination with size or other morphological traits, may affect nutrient benefits for hatchlings, as well as costs of production. Further comparative studies including chemical approaches will help us to understand the evolution and adaptation of trophic egg differentiation.

Ovarian dynamics

As in other subsocial insects (e.g., Rankin et al. 1995; reviewed by Trumbo 2002), ovarian development is suppressed or suspended during maternal care in subsocial Heteroptera (Eberhard 1975; Kudo et al. 1989; Kudo and Nakahira 1993; Parr et al. 2002). The ovaries of *A. triguttulus* females, however, showed active oogenesis and usually contained mature chorionated eggs and a series of developing oocytes during egg care.

Within 2 days after beginning oviposition, females laid 73.50 ± 16.26 (SD) eggs, and about 10 mature eggs were still retained in their ovaries at dissection (Fig. 4). Almost all the eggs laid (71.17 ± 15.61) were viable. During the 10 days between initial oviposition and hatching, females lay about 30 inviable trophic eggs (Kudo and Nakahira 2004), although the number of trophic eggs varies among females and between populations on different host plants (S. Kudo and T. Nakahira, unpublished data). Thus, at least some of the trophic eggs contained in clutches at hatching must have matured and been deposited continu-

ously during egg care. Females retained some mature eggs in their ovaries just before hatching (at day 10; see Fig. 4). No females lay viable eggs during brood care (Kudo and Nakahira 2004), and thus the retained mature eggs must have been trophic. These trophic eggs may be deposited at or soon after hatching.

In the *Lamium* spp. on which *A. triguttulus* depends, seed production and the distribution of seeds fallen to the ground vary greatly in time and space in the field (S. Kudo and T. Nakahira, unpublished data). Maternal provisioning of host seeds may not always be sufficient to support hatched nymphs and, therefore, nymphs may often face the risk of food shortages. Moreover, because of high predation pressure by ants in the myrmecophorous *Lamium* patches (Nakahira 1992), it would be risky for young nymphs to forage independently for seeds on the ground. Trophic eggs should be favoured by *A. triguttulus* in such variable and risky environments (Kudo and Nakahira 2004, 2005).

However, despite the spatial heterogeneities, the resource conditions within host-plant patches in which individual females feed upon developing seeds and develop their ovaries should be correlated with those for their offspring, which will later be fed with fallen seeds from the same patches. Thus, females may use resource conditions as predictable cues for making trophic-egg allocation decisions. In fact, as has also been shown in a ladybird beetle (Perry and Roitberg 2005), *A. triguttulus* females adjust their trophic-egg production in response to resource conditions, increasing the number of trophic eggs per viable egg in clutches experiencing poor conditions (Kudo and Nakahira 2005). Such adaptive allocation of trophic eggs can be achieved proximately using available nutrient reserves to adjust oocyte development.

Adomerus triguttulus females sometimes temporarily leave their clutches and feed upon host seeds during egg care (Nakahira 1992, 1994). The females initially lose body mass after the deposition of viable eggs, but usually recover it by the middle of the egg care period (Nakahira 1994). This recovery of body mass must be due to food intake. Reserves accumulated during egg care could be allocated to different reproductive options, i.e., maternal activities including trophic-egg production in the current breeding cycle as well as future breeding opportunities, if available. Resource availability in the field would be constantly changing, even during a given egg period; newly mature seeds would be supplied from host plants, whereas fallen seeds could be carried away by ants or fed upon by other seed-eaters (Nakahira 1992). It is quite possible that resource conditions affect trophic-egg production not only before oviposition but also during egg care. Continuous trophic-egg maturation may allow females to monitor changing resource conditions and enable them to achieve more flexible and adaptive allocations of parental investment.

Acknowledgements

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